EMPIRICAL MODELS OF STEM GROWTH AND VASCULATURE DIFFERENTIATION PROCESSES

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Abstract. A new notation for leaf trace patterns was developed which is consistent with contemporary contact parastichy phyllotaxis notation. New computer-aided methods for generating accurate stem tissue maps were developed. Study of the tissue maps for the various leaf trace patterns exhibited by Linum stems through ontogeny generated a set of observations which permits more rigorous definition of the developmental rules for vascular pattern formation. Changes in Linum stem growth through ontogeny was defined by empirical models generated by computer-aided analysis of scanning electron micrographs. Linum stems undergo progressive changes from low order to higher order patterns of leaf trace interconnections and phyllotaxis through ontogeny. Positional relationships between interconnected leaf traces is found predictable using long-known geometric principles of phyllotaxis.

Keywords. Leaf trace patterns; phyllotaxis.

INTRODUCTION

Nearly every report that has addressed leaf trace pattern (LTP) includes a statement that the vascular patterns are related to the phyllotaxis of various stems. Curiously, however, with the notable exceptions of Sterling (1945) and Namboodiri and Beck (1968) no attempts have been made to rigorously define this relationship. One of the major difficulties in defining such a relationship is the disparity between the methods of notation employed by students of leaf arrangement and students of leaf trace patterns.

Classification of LTP's has usually been by a modified divergence fraction notation from phyllotaxis. Divergence fraction notation was developed by Braun and Schimper (1835) to describe the arrangement of leaves about the mature stem axis. A given pattern of leaf arrangement was specified by determining the ratio of the number of turns around the stem axis between two successive foliar members of the most apparent orthostichy to the number of leaves between these members. An orthostichy is defined as an imaginary line drawn through leaves that are vertically above one another on the stem axis. The modified divergence fraction used to designate LTP is usually formed by citing the plastochron or age difference between leaves that are interconnected by central leaf traces as the denominator of the divergence fraction, and the number of gyres the generative spiral makes about the stem between these leaves as the numerator.

The regular organization of leaves about the plant stem has been recognized since the time of Theophrastus (Adler, 1974). Divergence fraction notation (Braun and Schimper, 1835) was based on the assumption that the generative spiral could adequately be modeled as a Spiral of Archimedes. Church (1901) cogently argued that the generative spiral is better defined as an equiangular or logarithmic spiral when one considers the arrangement of leaf primordia at the level of the shoot apex where phyllotactic pattern originates, since this spiral approximates active growth processes of the shoot apex more closely than does a Spiral of Archimedes. Furthermore, in spiral systems of phyllotaxis, parastichies, but not orthostichies, can be recognized at the level of the shoot apex. Parastichies are imaginary spirals that pass through series of leaves that differ by a constant number of plastochrons (e.g., passing through the 1st, 4th, 7th, 10th, ... leaves in sequence in the case of the 3-parastichy). Church (1901, 1904, 1968) introduced parastichy notation for phyllotactic description, which has been used in various modified forms by subsequent workers. Most contemporary students of phyllotaxis employ some form of intersecting parastichy notation to identify two sets of leaves that occur in specific relationships to one another at the level of the shoot apex when specifying patterns of leaf arrangement. A synthesis of the geometry of systems of intersecting parastichies has been recently provided by Erickson (1983).

A new notation for LTP designation is proposed, herein, which is consistent with contemporary parastichy phyllotaxis notation and adequately reflects the interconnections among leaf traces within stems. This is the first step toward clarifying the relationship between LTP and phyllotaxis.

Most reports on LTP present these patterns in the form of diagramatic line drawings representing procambium or vasculature tissue only. The inconsistencies among the line drawings of LTP of various workers has been cogently addressed by Beck, Schmid and Rothwell, 1982. Understanding the relationship between leaf trace pattern formation and phyllotaxis becomes more manageable when all tissues of the entire stem are examined as a unit.

A new method is introduced, herein, which employs computer-aided generation of accurate tissue maps from serial transverse stem sections. This method not only provides a means of depicting procambial and/or residual meristem tissue, but the various parenchyma tissue of the stem as well.

METHODS

Terminology. The terminology used in this report is that defined by Beck, Schmid and Rothwell (1982) with the following exceptions. The term, axial bundle, is not used since, as Allsopp (1964) pointed out, discussions as to which part of the

vascular system is cauline and which is of foliar origin are futile, the distinction being manifestly artificial in a continuous system. Sympodium is thus taken to mean a group of interconnected leaf traces. The term leaf gap is used in reference to parenchyma within the vascular cylinder in acropetal association with a leaf trace that is diverging from the vascular cylinder. The term interfascicular ray is used in reference to parenchyma within the vascular cylinder in tangential association with a leaf trace. Parenchyma comprising leaf gaps and interfascicular rays form a continuous region of tissue at the nodal point of entry of any particular leaf trace, hence these terms refer to the spatial positions of this tissue relative to a leaf trace. The terms anodic, meaning same direction as, and cathodic, meaning opposite direction to the generative spiral (Girolami, 1953) are used instead of sinistrose and dextrose in describing spatial relationships between leaf traces.

Two broad tissue categories were recognized in the initial data collection phase of this research: 1) Residual meristem/procambium (RMPC), defined by cells that had densely stained protoplasm with no noticeable vacuolation. The term "unclaimed RMPC" was later used in reference to portions of the RMPC which had no clear longitudinal association with existing leaf primordia. The term "leaf trace" was later used in reference to portions of the RMPC that had longitudinal association with leaf primordia. 2) Parenchyma (P) was defined by cells that exhibited vacuolation of at least one quarter of their cross sectional areas. The terms "pith," "interfascicular rays," "leaf gaps" and "cortex" were later used in reference to different spatial regions of the P tissue.

Data Collection. Random samples of 10 flax plants each were made from large populations of plants at 24, 48, 72, 96 and 120 h after seed sowing and when leaves at nodes 1, 2, 3, 4, 5, 10, 15 and 30 were visible at the terminal shoot apex. Nodes were numbered in their order of appearance in ontogeny with number 1 being assigned to the first node above the cotyledonary node. Entire stems including hypocotyls were transversely sectioned at 8 μm for seedling material; whereas only the terminal 3.0 cm of the shoot apices were transversely sectioned at 10 μm for plants within the last three sample groups. Sectioned material was carefully screened for orthogonal orientation of the longitudinal stem axis to the plane of sectioning and three specimens exhibiting little or no skewness were analyzed at each sample time. A nodal plane was defined as that section in which a particular leaf primordia was at least 85% attached with the stem axis and the three procambial bundles within the leaf lamina had converged. Internode lengths between all nodes in a specimen were determined by section counts between successive nodal planes on a stem.

Photomicrographs were made at mid-internode levels, defined as the section midway between two successive nodal planes, for all nodes on a given specimen. In early seedling specimens, additional photomicrographs were made at periodic intervals throughout the hypocotyl. Coordinates for data points marked on each micrograph, as described below, were collected via a HIPAD digitizing tablet interfaced with a Microtechnology 130-2D computer. BASIC computer programs entitled UNROLLSTELE and BIUNRLSTELE were written to generate the quantitative data used in the mapping procedure for stems with spiral and bijugate leaf arrangement, respectively. The only difference in these two programs was the algorithm used in aligning successive sections to coincidence, as described below.

Section alignment. The centers of the central procambial bundle of five successive leaf primordia which had diverged from the vascular cylinder were marked on specimens with spiral leaf arrangement. These primordia were specifically selected to avoid alignment bias due to displacement of procambial regions within the vascular cylinder at positions of leaf trace divergences. These points were digitized and the sequence number of these primordia were entered into the computer for each section level.

The radii between these five points and the center of the stem, and the divergence angles between successive points were calculated via the technique developed by Maksymowych and Erickson (1976). While this technique provides good estimates of radii and angles, it does not permit estimation of the coordinates of the center of the stem in digitizer space. The digitizer coordinates for the stem center were determined by solving for the common point of intersection of circles centered about each primordia center point and with radii equal to the distance between primordia center points and the stem center as shown in Fig. 1.

Once the central stem coordinates (XC,YC) were known for a given section, all data of that section were translated such that (XC,YC) corresponded with the digitizer origin (0,0). All data for a given section were then converted from rectangular coordinates (X,Y) to polar coordinates (ρ, ϕ).

Data from successively basal sections of a specimen were rotated to coincidence by a counter-clockwise rotation through an angle equal to the mean difference between the angular coordinates of each primordia seen in both sections. On average, this mean angle of rotation was determined on the basis of four primordia that were visible at two successive section levels. Repetition of these steps for each section of a specimen resulted in a precise alignment of successively basal sections to coincidence on the basis of morphological features that were independent of the positions of internal stem tissues.

The alignment algorithm for stems exhibiting bijugate leaf arrangement with divergence angle = 90° between successive leaf pairs (decussate phyllotaxis) was slightly different. Members of each leaf pair were always 180° opposed to one another. In such plants, the center coordinate (XC,YC) was calculated as the mean of half the distance in digitizer space between center coordinates of uninserted leaf primordia pairs from two successive nodes. The data for a section was then translated such that (XC,YC) = (0,0), followed by polar conversion and subsequent rotation of the data as described above. This alignment algorithm was unbiased for all sections above the cotyledonary node. However, since there were no bundles external to the vascular cylinder in the hypocotyl region of the plants, the central cotyledonary procambial bundle and the procambial bundles for the first node within the vascular cylinder were used as alignment points in this region of young seedling specimens. This procedure introduced alignment bias that masked any tangential displacement of the procambial bundles in the hypocotyl regions of the plants but did not obscure the pattern of confluence between these bundles.

Tissue analysis. Five points in association with each RMPC sector visible in a particular section were digitized in the following sequence. Points 1 and 2 were located at the tangential boundaries of RMPC and P regions. Points 3 and 4 were located on the radial boundaries of RMPC and P regions midway between points 1 and 2. Point 5 was located on the surface of the epidermis and in radial alignment with points 3 and 4.

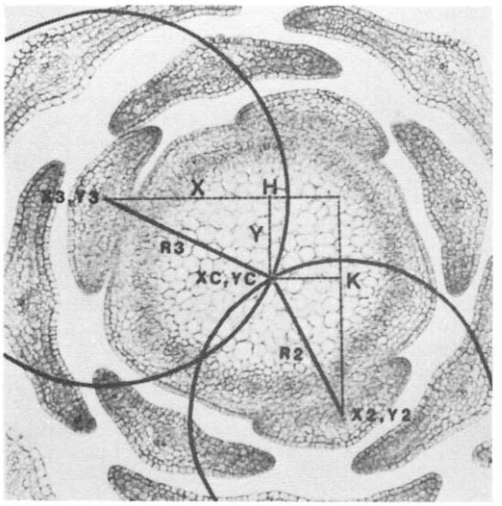

Fig. 1. Given that the coordinates X2, Y2 and X3, Y3 and distances R2, R3 are known, solve for the coordinates XC, YC. If we let X = XC - X3 ; Y = YC - Y3; and H = X2 - X3 ; K = Y2 - Y3. Then solve the quadratic $4(H^2 + K^2)X^2 - 4ZHX + Z^2 - 4K^2R3^2 = 0$; where $Z = R3^2 + H^2 + K^2 - R2^2$; Then XC = X3 + X. Furthermore, Y = (Z - 2HX)/2K) by substitution, and YC = Y3 + Y. Since only XC and YC are points common to intersections of the circles centered about all five primordia, the other possible coordinates for the quadratic solution above can be eliminated by selection of the coordinates with the least differences between them. The above procedure provides the first objective definition of the stem center in geometric terms.

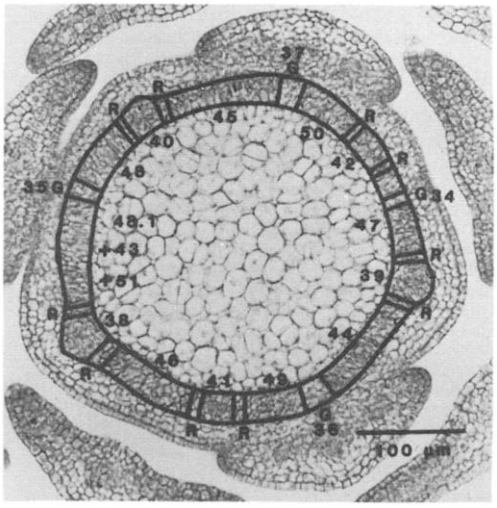

Fig. 2. Subdivision of flax stem into tissue categories. Inner circle represents P tissue of pith. Innermost annulus represents vascular cylinder, subdivided into RMPC tissue (numbered) and P tissue of leaf gaps (G) and interfascicular rays (R). Outermost annulus represents P tissue of cortex and epidermis.

Methods of analytic geometry permitted calculation of the stem tissue dimensions from these groups of five points in association with the RMPC sectors as follows.

1. RMPC Arc = $\phi 1-\phi 2$
2. P Arc within Vascular Cylinder = $\phi 2-\phi 6$
3. Pith Radius = $\rho 3$
4. RMPC Radius = $\rho 4-\rho 3$
5. Cortex Radius = $\rho 5-\rho 4$
6. Intra-RMPC Sector Length = $[\rho 3+((\rho 4-\rho 3)/2)](\phi 1-\phi 2)$
7. Inter-RMPC Sector Length = $[\rho 6^2+\rho 2^2-2(\rho 6\rho 2)\cos(\phi 1-\phi 6)]^{\frac{1}{2}}$
8. Pith Sector Area = $[\rho 3[[\rho 3+((\rho 4-\rho 3)/2)](\phi 1-\phi 2)]]/2$
9. RMPC Sector Area = $0.5(\phi 1-\phi 2)(\rho 4+\rho 3)(\rho 4-\rho 3)$
10. Cortical Sector Area = $0.5(\phi 1-\phi 2)(\rho 5+\rho 4)(\rho 5-\rho 4)$

As shown in Fig. 2 these methods subdivide the stem tissue into a cylindrical P pith region and two annuli; the innermost representing RMPC and P tissue of the vascular cylinder, the outermost representing P tissue of the cortex and the epidermis. The parenchyma of the vascular cylinder annulus was either ray parenchyma (R) on either side of a leaf trace; or leaf gap parenchyma (G), acropetally above a leaf trace. Since the section level and the sequence number of each arc sector were known, these data could be further examined either on the basis of individual tissue sectors of known plastochronic age, or integrated at each section level to provide information on all the tissue of one type at a particular section level.

LTP notation. The new notation J(m;n)/D was developed to describe leaf trace patterns in flax stems, where: J = jugacity, or number of leaves per node; (m;n) = the plastochronic age differences between leaves that were interconnected by juncture of their traces. It should be noted here that some traces only interconnected with one other trace, while others interconnected to three; in these cases the notation (m) and (m,n,o) were employed. D = the plastochronic age difference between a bifurcated leaf trace and the leaf subtending the bifurcating leaf gap. In cases where bifurcation does not occur, /D was simply omitted.

Stem growth. A complete description of flax stem growth appears in Meicenheimer, 1986b. The pertinent features that relate to changes in LTP and phyllotaxis through ontogeny, can be summarized as follows. There was a progressive decrease in the plastochron or length of time elapsing between leaf primordia initiations from an initial 35 hr interval toward a plastochron equal to 5 hours. There was also a progressive decrease in the relative plastochron rate of radial shoot expansion from an initial rate of 35%/plastochron toward a final rate of 5%/plastochron. The relative plastochron rate of vertical stem expansion was slightly higher than the relative radial rate of stem expansion throughout flax development but it also exhibited a decrease from an initial value of 54%/plastochron toward a final value of 15% per plastochron. In parallel with these decreases in relative plastochron rates of stem growth the size of the shoot apical meristem increased throughout development as indicated by the time course for initial shoot meristem radius and initial shoot meristem height. Least squares regression on log values of these data indicate that there is about a 2% decrease in relative plastochron rates of stem growth and about a 1% per plastochron increase in initial shoot apical meristem dimensions throughout ontogeny. The patterns of phyllotaxis exhibited by Linum stems through ontogeny were characterized by Richards' Phyllotaxis Index (Richards, 1948) as indicated in Table 1.

TABLE 1. Divergence angle (α), relative plastochron rate of radial stem growth (K_r) and Richards' Phyllotaxis Index (RPI) for flax stem with indicated number of total nodes (TN).

TN	α^0	K_r	RPI
1-4	109.5	0.37	2.28
5-9	127.6	0.18	3.01
15-30	137.0	0.08	3.92
32-34	138.7	0.07	4.03
35-80	137.4	0.05	4.30

DISCUSSION AND CONCLUSIONS

General LTP rules. A series of eight tissue maps that depict the basic LTP's exhibited by flax stems throughout ontogeny appear in Meicenheimer (1986a). Examination of the details of all these maps reveals that the following characteristics are common to the delimitation of all leaf traces regardless of the LTP: 1. Within the shoot apical meristem there are large angular sectors of RMPC underlying presumptive sites of primordia initiation; a fraction of one of these sectors becomes separated tangentially from the remainder via appearance of vacuolated P cells of the interfascicular rays on either side of the newly formed leaf trace and acropetally from the remainder via appearance of vacuolated P cells comprising the associated leaf gap. 2. Further delimitation of any given leaf trace is associated with simultaneous longitudinal expansion of the population of parenchyma comprising the leaf gap and that comprising the interfascicular rays in opposite directions relative to the nodal region where these two parenchyma populations are spatially continuous. 3. Interrelationships between the interfascicular rays and leaf gaps associated with existing leaf traces result in isolated sectors of unclaimed RMPC within the shoot apex. 4. The pattern of leaf trace interconnections at any stage of ontogeny is delimited by the interrelationships existing between the parenchyma of leaf gaps and interfascicular rays associated with leaf traces of existing leaf primordia.

Jean (1982) discusses vascular trace patterns in terms of hierarchical control of phyllotaxis, by which he means those rules or constants that arise within a collection of elements, but which affect individual elements of the collection (Pattee, 1970). In the broad sense of this definition, the phenomena described in the points 1-4, above support Jean's interpretation. The vascular trace maps presented by Jean (1982) in support of hierarchical control, however, are not consistent with maps and rules discovered for Linum LTP. For example, the bifurcation induction lines originally proposed by Bolle (1939) and expounded upon by Jean (1982) appear to have no counterpart in the flax vascular system. Rather, the phenomena described in points 1-4 above appear to explain the observed patterns of leaf trace interconnections.

Changes in LTP through ontogeny. Consideration of the flax LTP's throughout ontogeny as summarized via the vascular tissue maps (Meicenheimer, 1986a) reveals: 5. The flax leaf trace vasculature consists of two separate sympodia until differentiation of leaf trace 10 in a (3;5)/8 LTP in plants undergoing spiral transformation of phyllotaxis at node 2; thereafter the LTP is best described as a "closed" vascular system of one sympodium. The "open" condition of the intial LTP results from the existence of confluent regions between the leaf gap and interfascicular ray parenchyma associated with different leaf traces. The "closed" condition arises when this region of confluence is interrupted by the apparent failure of the RMPC to differentiate into parenchyma; thereby resulting in an asymmetric bifurcation of developing leaf traces. 6. In 72 h seedlings with stems exhibiting decussate or spiral phyllotaxis, the initial 1 traces are contiguous with traces in the anodic and cathodic locations. The longitudinal extent of the parenchyma associated with these traces varies depending on the phyllotaxis. This presumably is due to the difference in the initial timing of the events described in point 1. above. Therefore, the variation in early 72 h seedling LTP reflects the differences in the number of leaves per node and the angular relationships between these leaves. 7. In accordance with the proposed LTP notation, the flax stem undergoes a progressive change from a (1;2)$\longrightarrow$ (2;3)/4 $\longrightarrow$ (3;5) $\longrightarrow$ (3;5)/8$\rightarrow$ (3;5;8)/8/13 $\longrightarrow$ (5;8)/13 leaf trace pattern. The last LTP appears to be stable from ca. the twenty eighth plastochron up to at least the eightieth plastochron. 8. The number of discrete unclaimed RMPC sectors increases from four in the early seedling stages to five in the intermediate stages to six in the older stages of flax ontogeny. These discrete sectors always formed confluent regions of RMPC tissue in the more acropetal regions of the SAM and were always confluent with leaf traces in the basipetal region of the SAM. 9. The angular sector occupied by a leaf trace decreases as higher order patterns of LTP are produced.

In conclusion, then, the changes that occurred in leaf trace patterns are explained in part by the change that occurs in the divergence angles between successive primordia initiated on a shoot apical meristem. Parallel with these angular changes there is a progressive decrease in the angular sector commissioned from the unclaimed residual meristem region of the shoot apical meristem which is expanding in size as higher orders of LTP are formed. Furthermore, the progressive changes that occurred in both the contact parastichy patterns of phyllotaxy as indicated by Richards' Phyllotaxis Index and the leaf trace patterns as indicated by the current notation from low order patterns at early stages toward higher order patterns at later stages of ontogeny resulted from progressive decreases in the relative plastochron rates of radial and vertical stem growth plus parallel decreases in the plastochron. There is thus no change in the chronological rates of stem growth through ontogeny, rather only the relative points of leaf primordia initiation change, giving rise to new patterns of leaf arrangement. The differentiation of parenchyma within the interfascicular rays and leaf gaps associated with existing leaf primordia which exhibited such shifts in their relative positions through ontogeny give rise to new LTP.

LTP and phyllotaxis relationship. Namboodiri and Beck (1968) following Sterling (1945) attempted to define the relationship between the vascular system and phyllotaxis by the following three criteria: 1. Direction of the generative spiral. 2. Angle of divergence. 3. Number of sympodia. These workers correctly pointed out that if the above three criteria were known, then Sterling's (1945) fourth suggested criteria, the direction of trace linkages, was redundant. They present a diagramatic argument that illustrates that the direction of trace linkages can be predicted on the basis of the above three criteria. They express both LTP and phyllotaxis in the divergence fraction notation. Utilizing contact parastichy notation for phyllotaxis and the proposed LTP notation it is possible to further generalize the above criteria for the relationship between patterns of leaf arrangement and leaf trace interconnections as follows.

Van Iterson (1907) formally developed the geometric relationships between members of regular points on cylinders, planes, and cones. He established that the angular relationships between successive members of a m-parastichy in such systems can be expressed by: $m\alpha = \Delta m\ 2\pi + \delta m$; where m = parastichy number; α = divergence angle (radians); Δm = encyclic number = number of turns, rounded to the nearest integer, which the generative spiral makes between 0 and the mth member of the system; δm = secondary divergence = small angle (+ or -) which corrects the equation for inclusion of the integer encyclic number. The secondary divergence (δm) is thus an angular correction between the artificial orthostichy (expressed by $\Delta m 2\pi$) and the actual parastichy describing the position of members arranged in regular arrangements. The sign of δm determines whether the mth number along the parastichy will be anodic (+) or cathodic (-) relative to the 0 or older member of the parastichy. This relationship is completely independent of the chirality of the generative spiral. Since it has long been recognized (cf. Sinnot, 1960) that the chirality of the generative spiral for a given plant occurs with equal frequency in both directions and that generative spiral chirality is not an inherited quality, it seems desirable to exclude this parameter from consideration of LTP-phyllotaxis relationships. The above formula effectively does this. In order to test the accuracy of the formula a divergence angle of 137.5^{0} was assumed and the secondary divergence calculated via formula (1) for sequential members of the Fibonacci series. These calculations result in $\delta_2 = -85^{0}, \delta_3 = 52^{0}, \delta_5 = -32^{0}$, and $\delta_8 = 19.28^{0}$. The alteration cathodic, anodic, cathodic, anodic is exactly the relationship that was observed in the flax stems.

From these considerations, it is proposed that the criteria for establishing the relationship between LTP and phyllotaxis suggested by Namboodiri and Beck (1968) can be reduced to: 1. knowledge of the divergence angle and 2. knowledge of whether leaf gaps and interfascicular ray parenchyma associated with different leaf traces are contiguous (open system) or not (closed system). The relative positions of confluent leaf traces can be determined on the basis of the sign of the secondary divergence angle from the equation above.

LTP notation. The new notation proposed for LTP designation accurately conveys all leaf trace relationships and is consistent with the contact parastichy notation for phyllotaxis. This consistency permits application of mathematical facts known from phyllotaxis to be applied to problems of leaf trace patterns, as illustrated above. This notation should prove useful to considerations of functional relationships between leaves on plant stems. For example, in plants with (3;5)/8 LTP, leaves that differ in age by multiples of 3 and 5 plastochrons are directly interconnected via their leaf traces and leaves that differ in age by multiples of 8 = (3 + 5), 11 = (8 + 3) and 13 = (8 + 5) plastochrons are indirectly interconnected via their leaf traces.

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